

HIBERNATION OF THE THIRTEEN-LINED GROUND
SQUIRREL CITELLUS TRIDECIMLINEATUS
(MITCHILL)

V. FOOD, LIGHT, CONFINED AIR, PRECOOLING, CASTRATION AND
FATNESS IN RELATION TO PRODUCTION OF HIBERNATION ¹

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INTRODUCTION

The cause of hibernation has been considered by many investigators and to account for it there has been presented a large number of theories, some based upon extended observations, others founded upon more or less casual studies of a small number of animals. In few instances have carefully controlled experiments been conducted. Most of these theories have been brought together by Rasmussen (1916).

Several authors admit that starvation tends to produce hibernation (Mangili, 1807; Hall, 1832; Merzbacher, 1904; Simpson, 1912; Mann, 1916; Shaw, 1925; and others). Most of these also state that little food was eaten shortly before a mammal goes into hibernation, indicating that hibernation took place when food was present and that starvation was not a factor. Dry food is considered a cause of aestivation (which is apparently a condition of lowered metabolism accompanied by a drop in body temperature, as in hibernation, but of a less degree and occurring in the summer or fall instead of in the winter) by Shaw (1925), Kashkarov and Lein (1927) and Kalaboukhov (1929).

Vitiated air was not considered as having any effect on hibernation in marmots by Mangili (1807), but Bert (1868, 1870) was able to produce lethargy in dormice by placing them at a low temperature in a bell jar deprived of air.

There appears to be an agreement among those authors who have mentioned adiposity that this condition is common in the fall among hibernators and that such a condition is favorable to hibernation, *e.g.*,

¹ Contribution 118 from the Department of Zoölogy, Kansas State Agricultural Experiment Station, Manhattan, Kansas. Earlier papers in this series deal with conditions in hibernation (Johnson, 1928), waking from hibernation (Johnson, 1929*a*, 1929*b*), and the influence of thyroxin, pituitrin and dessiccated thymus and thyroid on hibernation (Johnson and Hanawalt, 1930). For abstracts referring to portions of this work see Anat. Rec. 31: 337 and 37: 225.

Mangili (1807), Horvath (1881), Forel (1887*a*, 1887*b*), Mills (1892, 1893), Claparède (1905), and Mann (1916). According to Rasmussen (1916), this view was also presented by Sacc (1858).

No study has apparently been made relative to the effects of light and darkness, precooling, or castration, although Mann (1916) usually placed his ground squirrels in the dark in addition to starving them and cooling the room when he wished to produce hibernation.

The present work was begun in 1925 and has been continued to 1930 as time and numbers of animals available have permitted. Ground squirrels of the variety *Citellus tridecemlineatus pallidus* Allen from western Kansas were used. Since this variety has been broken up by Howell (Proc. Biol. Soc. Wash., 41: 211), it would seem that some at least of the animals used would belong to the southern group (*C. t. arenicola*) of what has previously been taken as all belonging to the variety or subspecies *C. t. pallidus*. Large numbers of ground squirrels could usually be obtained, so that the data of the different experiments could be treated statistically, thereby eliminating, to a large extent, personal judgment. Furthermore, for each animal placed under experimental conditions, another of like weight and sex was usually placed under conditions that were identical except for the one factor being tested, *e.g.*, food, confined air, etc. Observations soon showed that there was considerable individual variation and that the use of large numbers was necessary in order to make the results reliable. The work was done partly in a refrigeration room in which there was some daily fluctuation of temperature, but chiefly in an automatically controlled electric refrigerator in which there was very little fluctuation of temperature.

EXPERIMENTAL

Starvation and Darkness

These two conditions were studied together in nineteen experiments, from January to October, 1925. Each experiment lasted between 7 and 23 days. Three ground squirrels were fed in the light, three were fed in the dark, three were starved in the light, and three were starved in the dark. The starved animals were given water, green feed and, in most of the experiments, five kernels of corn daily. The fed animals were given water, green feed and liberal quantities of oats, with some wheat or corn at times. The light which was used to illuminate half of the cages was furnished by one 100-watt and one 50-watt electric bulb which were kept going throughout the experiments. The lights were at a distance of about six feet from the cages. The temperature of the cold room, which was approximately a ten-foot cube, showed an average range of daily fluctuation of 6° C.

At the end of an experiment the 12 animals were removed to the heated animal house and fed daily. Usually these were returned to the cold room in a new experiment in about two weeks and given treatment opposite to that in their previous period to balance out individual tendencies if there were any. It also avoided starving any animal at close intervals.

TABLE I

Food and light in relation to hibernation. Summary of daily records in the cold room.

The total days that the three animals were in the refrigeration room are given within the parentheses; the total days before hibernation for each group of three are given before the parentheses; the latter divided by the former gives the percentage of days before hibernation for each group of three animals and is given in the per cent column.

Date begun 1925	Time in days	Fed and light		Fed and dark		Starved and light		Starved and dark	
		Total days	Per cent	Total days	Per cent	Total days	Per cent	Total days	Per cent
Jan. 6	7	20 (21)	95	6 (21)	29	10 (21)	48	0 (21)	0
Jan. 14	9	16 (24)	67	9 (25)	36	5 (22)	23	5 (25)	20
Jan. 24	11	2 (33)	61	17 (33)	52	8 (33)	24	15 (33)	45
Feb. 4	12	14 (36)	39	25 (33)	76	7 (36)	19	5 (33)	15
Feb. 17	13	39 (39)	100	33 (39)	85	12 (39)	31	24 (39)	62
Mar. 3	14	42 (42)	100	42 (42)	100	11 (42)	21	12 (42)	29
Mar. 19	14	42 (42)	100	29 (39)	74	10 (42)	24	24 (26)	92
Apr. 2	16	48 (48)	100	42 (42)	100	7 (48)	15	6 (14)	43
May 7	23	56 (69)	81	69 (69)	100	34 (66)	52	66 (66)	100
May 30	15	45 (45)	100	45 (45)	100	23 (45)	51	7 (45)	16
June 16	18	54 (54)	100	43 (54)	80	31 (54)	57	30 (54)	56
July 4	13	39 (39)	100	37 (39)	95	26 (39)	67	24 (39)	62
July 18	13	26 (26)	100	39 (39)	100	10 (26)	38	29 (39)	74
Aug. 2	13	39 (39)	100	39 (39)	100	15 (39)	38	15 (39)	38
Aug. 15	13	27 (39)	69	27 (39)	69	3 (39)	8	11 (39)	28
Aug. 30	12	24 (24)	100	18 (36)	50	6 (24)	25	7 (24)	29
Sept. 11	11	7 (33)	21	15 (33)	45	23 (33)	70	14 (33)	42
Sept. 22	15	33 (45)	73	30 (45)	67	26 (45)	58	16 (24)	67
Oct. 8	16	34 (48)	71	9 (48)	19	3 (48)	6	17 (48)	35
Total days		607 (746)		574 (760)		270 (741)		327 (683)	
Average percentages		81.4		75.5		36.2		47.8	

In tabulating and evaluating the results (Table I) the number of animals given the same treatment (*e.g.*, given feed in the light) is multiplied by the days duration of the experiment (7 in the first experiment, to 23 in the ninth) to obtain the total days in the cold room, given in parentheses. The days spent in the cold room by each of the three animals before going into hibernation are added to obtain the

total days before hibernation, placed before the parentheses. The latter divided by the former gives the percentage of days before hibernation. The totals of the experiments are brought together in Table II and the percentage of days before hibernation computed for each of the four conditions, fed and light, fed and dark, starved and light, and starved and dark. When the percentages of days before hibernation are compared, it is observed that both of the fed groups averaged much higher than the starved groups. Feeding therefore delays hibernation, or starvation hastens entrance into this condition. The two "dark" groups show no marked difference from their corresponding "light" groups. Light or darkness appears to play very little, if any, part, then, in inducing hibernation.

TABLE II

Summary of Percentages of Days Before Hibernation from Table I

Fed vs. Starved			Light vs. Dark		
Light.....	81.4	36.2	Fed.....	81.4	75.5
Dark.....	75.5	47.8	Starved.....	36.2	47.8
Averages.....	78.5	42.0	Averages.....	58.8	61.6

Summary of Percentages of Days in Hibernation from a Table Not Published

Fed vs. Starved			Light vs. Dark		
Light.....	10.9	48.0	Fed.....	10.9	15.2
Dark.....	15.2	36.8	Starved.....	48.0	36.8
Averages.....	13.0	42.4	Averages.....	29.4	26.0

The data have similarly been tabulated to show the percentage of days in hibernation as a different measure of the production of hibernation. Only the summary of this table is included in Table II. The average percentage of days in hibernation is much higher for the starved groups than for the corresponding fed groups, showing in a different way the effectiveness of starvation in the production of hibernation. Here also there is no marked difference between the two dark and the two light groups. The difference is still less when the average of the two light groups is compared with that of the two dark groups. Statistical treatment showed that the results between each fed group and its corresponding control was significant (Difference/Probable Error = 11.3 in one case and 6.3 in the other case). The difference

between the "light" and "dark" groups was not significant ($D/PE = 1.6$ and 2.4 , respectively).

It appears safe to conclude from these experiments that starvation is a condition favorable to the production of hibernation, whereas darkness is no more conducive to hibernation than artificial light of a strength such as is used in an ordinary well-lighted room. Whether ultra-violet light might stimulate the animals to stay awake has not been investigated.

Confined Air

Preliminary experiments in which some animals had been placed in half-gallon tin cans with tight lids in which were punched only two six-penny nail holes about 3.0 mm. in diameter resulted in death in some of the animals. Four such holes, however, appeared to admit sufficient air to prevent suffocation at refrigerator temperatures. In each experiment three animals were placed in the four-hole cans, three were placed in open wire cages (6 x 6 x 10 inches) as controls and three others were placed in half-gallon cans with highly perforated lids to admit an abundance of air. The latter controls were used to determine the effect, if any, of the limited space on the experimental (confined air) animals. Except in a few short preliminary experiments the animals were fed whole oats, wheat or corn, and a small amount of green grass or sprouted oats daily. Wood shavings were used as nest material and in the cans also served to absorb the moisture from the breath of the animal. Each experiment was usually terminated after 7 days. The animals were usually undisturbed except for the daily observations. All the animals were in the dark.

From Table III it is to be noted that in all four sets of experiments or periods the confined air animals went into hibernation sooner and stayed in more of the time than the animals in the open cages. A summary of the results of these experiments shows that those animals in confined air went into hibernation after 19 per cent of the total days they were in the refrigerator as compared to 49 per cent in the case of the open cage animals. These results are quite significant ($D/PE = 9.5$) in showing the retarding effect of free air upon entrance into hibernation. The confined air animals were in hibernation 68 per cent of the days in the refrigerator, whereas those in open cages were in hibernation only 41 per cent of the days. These results are also significant ($D/PE = 9.4$). The total differences of periods 1 and 2 (Table III) and also of periods 1, 2 and 3 were found to be significant.

The confined air animals also showed an earlier entrance into hibernation and more days in hibernation than did those in the cans with

TABLE III
Results of Confined Air Experiments

Period	Experimentals in Cans with four holes				Controls in cans with many holes				Controls in open wire cages			
	No. of Animals	Per cent of Days		No. of Animals	Per cent of Days		No. of Animals	Per cent of Days		No. of Animals	Per cent of Days	
		Before hibernation	In hibernation		Before hibernation	In hibernation		Before hibernation	In hibernation		Before hibernation	In hibernation
April 1925 to June 1925	18	15	74	—	—	—	16	81	15	16	81	15
Nov. 1925 to June 1927	50	20	66	51	33	46	51	39	49	51	39	49
June 1927 to Oct. 1927	27	14	73	25	55	37	25	52	38	25	52	38
Sept. 1929 to Feb. 1930	13	26	59	15	31	56	15	42	48	15	42	48
Total Period* April 1925 to Feb. 1930	108	19	68				108	49	41			
Period* Nov. 1925 to Feb. 1930	90	19	67	91	39	45	91	43	45			

* Owing to the difference in number of animals in the groups above, these percentages are not averaged from the above averages, but from a table which contains the percentages for each animal.

many holes. The percentage of days before hibernation was 19 in the case of the experimental and 39 in the case of the controls in the many-hole cans ($D/PE = 5$). The percentage of days in hibernation was 67 for the experimentals and only 45 for the controls in many-hole cans ($D/PE = 6.7$). These results show a significant increase in early entrance into hibernation and continuance in this state because of the confined air, and show that the limited space of the cans played little, if any, part in the production of hibernation in the four-hole cans. It is to be noted, however, that in the last experiments (13–15 animals) nearly as much hibernation occurred in the cans with many holes as in those with four holes. In the other groups of experiments which included larger numbers of animals this was not the case. In these last experiments two conditions were unfavorable to hibernation in the four-hole cans. One was that the refrigerator was running very little and did not freeze the condensed moisture in the refrigerator as in active refrigeration, resulting in a high humidity in the cans. The other was that the animals were placed in the four-hole cans just as soon as placed in the refrigerator. Furthermore, the temperature in the refrigerator was not as low as usual. In this connection it should be stated that one condition tending to retard hibernation in the four-hole cans, in most of the experiments, was the retention of heat in these cans as long as the animal was active, *i.e.*, not torpid. Observations showed the temperature to be higher in these cans than in the cans with many holes. In some cases the animal appeared to be irritated by the confined air if it did not soon become torpid, and in the last series of experiments some of the confined air animals died.

Two methods of lowering the temperature in the four-hole cans were tried. In one experiment these cans were placed on a shelf below the others which was not over one degree cooler. In three other experiments the four-hole cans were wrapped on the sides by a small towel and then set in a shallow pan of water. Evaporation tended to cool the can one to three degrees below the temperature of the cans with many holes when the animals were normal in both. To avoid overcooling the four-hole cans, it was deemed best to place them on the same shelf without additional cooling by wet towels, etc., and permit the higher temperature to be a handicap to hibernation. Confined air, therefore, is probably more effective in the production of hibernation than indicated by these experiments and doubtless aids production of hibernation in nature, since the animals plug the entrance into their burrows when they retire in the fall. The limited space played very little part in the production of hibernation, possibly because the animals

usually roll up in the nest whether in a large or small cage except when eating. Most of these animals did not actively try to escape from the cages or cans.

Precooling

Proponents of the view that hibernation is produced not by external conditions, but by an internal seasonal rhythm, have pointed to the greater difficulty in producing hibernation in the summer with artificial cold than in winter. While less tendency to hibernate in the spring and early summer than in the early winter has been noted by the author, it must be recognized that several external conditions may be different in the fall from those obtaining in the spring and summer. The effects of a previous season of hibernation, the poor condition of the wild animal when caught for early summer study, and the greater excitability of new wild animals also usually caught just before the summer experiments are in contrast with the conditions produced by keeping the animals one to several months for the study of winter hibernation. The observations made so far suggest that these conditions influence hibernation. In the summer, also, animals are likely to be removed directly from a warm room into a refrigerator, whereas in the fall they are often taken from a room which has a low and possibly fluctuating temperature. This precooling of the animal nightly in an animal house is almost unavoidable unless special pains are taken to control the temperature. Drops in room temperature to 60° or even 40° C. would not be unusual under ordinary conditions of heating.

The effect of this condition of daily precooling has been investigated in seven experiments. In each experiment 10 animals were taken to a cold cave or attic where the temperature averaged about 16° or 17° C. for an average of about eight hours in one experiment and 15 hours in the others for a period of about ten days. Ten controls were kept in the animal house at an average temperature of about 26° C. or about 80° F. The animals in the cave or attic occasionally became partly torpid, but controls in the animal house did not hibernate there.

After this preliminary treatment, the animals were all removed to a refrigerator kept at a temperature which was constant or changed very slowly. The average temperature was about 7 or 8° C. Experimental (precooled) and control animals were on the same shelf, and therefore under identical conditions. In the seven experiments (Table IV) a total of 62 precooled animals went into hibernation after an average of 35.5 per cent of their days in the refrigerator while the controls entered hibernation only after 60.5 per cent of their total days in the

refrigerator, indicating that precooling caused the animals to hibernate sooner. In the per cent of days in hibernation the effect of precooling was also evident, but not to the same extent. The precooled animals

TABLE IV
Precooling Experiments

Date	Precooled (Experimental) Animals			No. of days	Controls		
	No. of animals	Per cent days before hibernation	Per cent days in hibernation		No. of animals	Per cent days before hibernation	Per cent days in hibernation
1927							
Jan. 1	9	34	43	15	9	43	29
Jan. 12	10	42	44	13	10	75	20
Jan. 27	7	29	40	15	8	72	15
Feb. 15	10	41	30*	14	10	90	8*
1928							
Mar. 6	7	41	24*	8	9	72	9*
1929							
Nov. 7	9	35	43†	11	9	29	51†
Nov. 16	10	20	63	6	9	36	48
Averages‡		35.5	41.7			60.5	26.0

Below are those experiments in which less than three animals in either group (experimental or control) hibernated.

1927							
Mar. 2	9	81	8	14	10	93	3
Apr. 3	9	93	2	18	10	84	13
Apr. 27	6	100	0	7	6	100	0
1930							
Feb. 4	9	98	2	7	9	70	14

* Note low percentage of hibernation in February and March, yet the precooled animals entered hibernation much sooner than the controls.

† Both groups went into hibernation very quickly in this experiment. Controls had been partly precooled, as the room temperature fell to 21° C. or 13° C. each night. Experimentals were in a temperature over night which fell to 10–20° C.

‡ Averages from another table in which each animal is counted equally. Not an average of the group averages given above.

hibernated 41.7 per cent of their total days in the refrigerator, while the controls hibernated only 26.0 per cent.

The difference in days *before* hibernation of the two groups was quite significant ($D/PE=6.48$) and that for days *in* hibernation was fairly significant ($D/PE=3.88$). As the influence of the precooling would wear off in a few days after placing the animals in the refrigerator, more importance should be attached to the data of days *before* hibernation than those of days *in* hibernation.

It should be noted that precooling was conducive to increased hibernation in the months of November to January, with one exception in which the controls had been precooled slightly through inability to control the temperature of the animal house. Precooling was less or not at all effective in the late winter and spring months, the period in which the animals gave indications of increased sexual activity by enlargement of the testes, scrotum and penis in the male and by enlargement of the vulva in the female. While exact comparisons are difficult to make between hibernation at the different seasons, it may be stated that observations over a period of years indicate that spring is not as good a season for hibernation as is the summer.

These experiments would indicate that one cause of more hibernation in the winter than in summer in the laboratory is sometimes a physiological condition produced by external conditions such as intermittent cold which aids in the production of hibernation, providing other conditions are moderately favorable to entrance into hibernation. Intermittent cold may not play a great part in nature, since the daily range is not great between six inches and one foot in the ground (Bouyoucos, 1913, 1916; Sweezy, 1903, McColloch and Hayes, 1923), where most of the hibernating nests occur (Johnson, 1917). However, a daily range of 10° F. or more was frequently noted at the six-inch level by Bouyoucos (1916) in loam and clay in September, but the range was only about half as great in October, when the soil temperature was falling gradually. It seems probable, however, that the gradual cooling of the soil would have a similar effect to that of intermittent precooling in that it would prepare the animal for hibernation. Whether precooling or gradual cooling would eliminate mortality in hibernation in summer cannot now be stated, but general observations point in that direction. It should also be noted that Payne (1927) has found that preliminary cooling as well as dehydration enables insects to withstand more severe and longer periods of cold.

Castration

Since ground squirrels become sexually active very soon after they come out of hibernation and in the animal house begin to show enlargement of the external genitalia in late winter, it was thought that

waking from hibernation in the spring was possibly induced to some extent by the increasing activity and internal secretion of the gonads. To test this possibility, a number of male ground squirrels were castrated and after a time were placed in a refrigerator with uncastrated controls. Some animals were used several times. Each experiment usually lasted two weeks. In the first four experiments, consisting of 3 to 5 castrated animals with the same number of controls, from May to July, 1926, there was no hibernation in either castrated or control (uncastrated) animals. From July to December, 1926, five more

TABLE V

Effect of Castration upon Hibernation in Late Winter and Early Spring

No. of animals	Experimental (castrated) male ground squirrels				Control (uncastrated) male ground squirrels		
	Per Cent days before hibernation	Per Cent days in hibernation	Date begun	Days in refrigerator	No. of animals	Per Cent days before hibernation	Per Cent days in hibernation
			1927				
6		52	Jan. 13	28†	6		43
6		82	Feb. 11	13†	6		37
4		36	Feb. 24	70†	4		13
4	42	43	Mar. 22	50	4	92	6
			1928				
3	0	78	Jan. 30	15	2	25	51
2	32	47	Mar. 8	19	1	28	51
1	100‡	0	Apr. 16	12	1	100‡	0
Av. 2.5	44	42		24	2	61	27
Average of individual records	27.6	55.6				46.2	33.6

† Continuation of a previous experiment.

‡ Animals thin, a condition tending to prevent hibernation.

experiments, and in August and September, 1927, two more experiments were performed in which there was an average of 34.5 per cent of days in hibernation in the 48 castrated males and 35.3 in the 46 uncastrated males, showing no effect of castration on hibernation in the summer, fall, and early winter.

Experiments performed from January to March, 1927, and January to April, 1928, showed an inhibitory effect of the gonads upon hibernation at this time of year (Table V). The castrated males showed 55.6 per cent days in hibernation, whereas the controls showed only 33.6 per cent days in hibernation in this experiment. The difference

is probably significant ($D/PE = 3.52$) because in other experiments normal males have not hibernated much at this time of the year and because a castration experiment with females at this time of year resulted similarly. In five experiments (January to March), with an average of 3 animals in each, the spayed females hibernated 45 per cent and the normal females only 30 per cent of the days in the re-

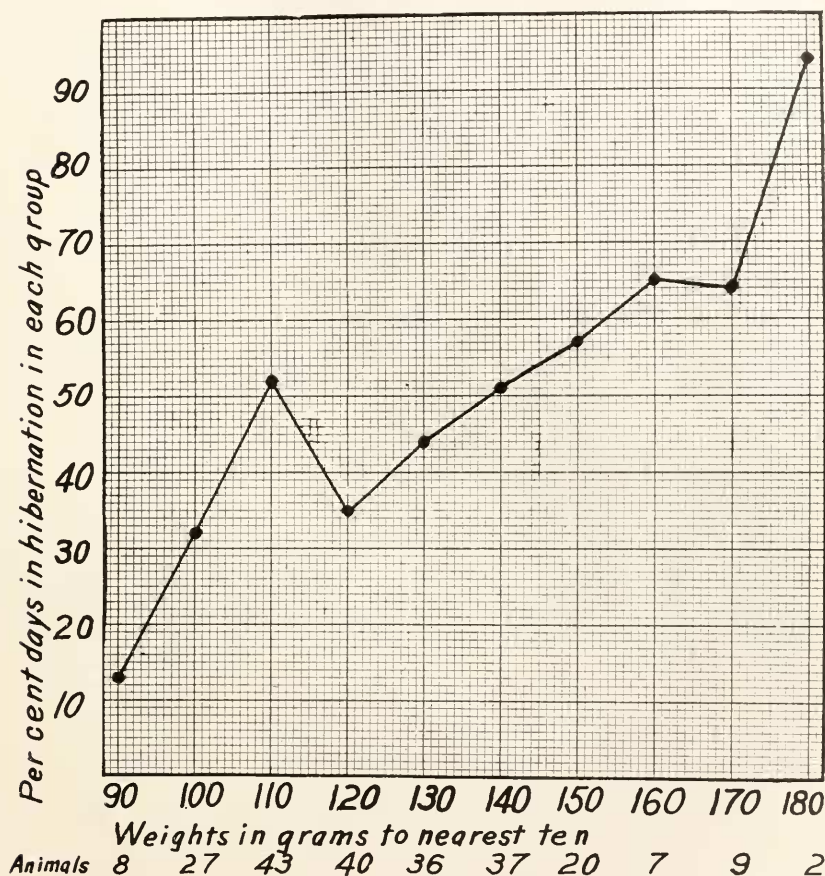


FIG. 1. Graph showing relation of weight to tendency to hibernate in ground squirrels. The bottom row of figures gives the number of animals having the weight given directly above.

frigerator. The spayed animals were in the refrigerator 34 per cent of the total days in the refrigerator before they hibernated whereas the controls were in the refrigerator 45 per cent of the total days before they hibernated. As the number of females is small and the difference not so striking as in the case of the males, these data were not treated

statistically. They lend support, however, to the data on the males as the results point in the same direction. It is not improbable that the increased sexual activity which is apparently in part responsible for lack of hibernation in spring is in turn caused by increased activity of the anterior pituitary. Work (unpublished) on the relation of this gland to hibernation has been in progress at this laboratory since 1926.

Weight and Hibernation

As weights were taken before and after each experiment in the refrigerator, it was possible to use existing data for a determination of the relationship between weight and hibernation. From these data the graph in Fig. 1 was made. Thirty-eight heavy animals weighing between 146 and 185 grams hibernated 62 per cent of the total days in the refrigerator, while 118 light animals weighing between 86 and 125 grams hibernated only 39 per cent of the total days in the refrigerator. Treated statistically, this is a significant difference ($D/PE = 5.7$). The number of days before hibernation took place was only 16 per cent of the total days in the refrigerator in the case of the heavier animals but was 41 per cent in the case of the leaner animals. This difference is also significant ($D/PE = 8.1$). It is to be seen, however, that there was not a perfect gradation of per cent of days of hibernation (Fig. 1) from the lightest to the heaviest animals; thus 43 animals weighing between 106 and 115 grams (given as 110 grams in the graph) hibernated more than another group of 40 animals weighing 10 grams more, but a predominance of high percentages of days *in* hibernation is found in the heavier groups and there is a predominance of high percentages of days *before* hibernation in the lighter groups.

SUMMARY

Controlled experiments performed on large numbers of ground squirrels showed that individuals starved or given very limited rations went into hibernation sooner and hibernated longer than those receiving an abundance of food. Moderately bright illumination with electric light did not affect the tendency to hibernate in any way. Confined air and precooling the animals nightly both aid in the production of hibernation. Castration does not influence hibernation except during the breeding season in the spring when castrated males hibernate more readily than normal males. The few spayed females used also hibernated more than the normal females in the spring. Obesity is favorable to hibernation.

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